

# THE LOWER PALAEOZOIC ECHINODERM FAUNAS OF THE BRITISH ISLES AND BALTO-SCANDIA

by G. REGNÉLL

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## INTRODUCTION

A GREAT many difficulties are involved in dealing with the relations between the British and the Balto-Scandian echinoderm faunas in Early Palaeozoic times. It is obvious that this is due mainly to two circumstances: the imperfect knowledge of the original composition of the faunas in different areas, and the insufficient exactitude in stratigraphic correlation between the British Isles on the one hand and Scandinavia, Estonia, and the Leningrad district on the other. It is not necessary to review here the various factors which in the course of time have acted upon the consecutive marine biota of different ecological niches and which have been decisive of the nature of the fossil record now available to us. Even Charles Darwin in his *Origin of Species*, the centenary of which is celebrated this year, devoted a special chapter to these questions which have subsequently received much attention in the literature. The essence of the dilemma was formulated by Wachsmuth and Springer (1897, p. 167) as follows: 'The trouble is that all our generalizations are necessarily based upon the Crinoids as they are represented in *our museums*, and not upon the Crinoids as they actually existed in geological time, which is a very different thing.' The term 'Crinoids' may of course be substituted by the name of any other group of echinoderms, or by the name of almost any other fossil group.

Wachsmuth and Springer introduced the human factor which should certainly not be neglected. It is a fact that some fossil groups have been subject to a more extensive collecting and a more penetrating study than other groups. Rather trivial matters have played a role in this respect. Henbest (1952, p. 304) observed, for instance, that the 'location of fossil records in relation to centres of education, research, industry, and mining is an important factor in the discovery and description of faunas'.

## LITERARY BACKGROUND

Much basic knowledge of Palaeozoic echinoderms has come from London—in the first place I refer to the brilliant work of F. A. Bather. However, apart from the carpoids and cystoids from the Ashgillian Starfish Bed of Ladyburn near Girvan described in his magnificent and very important memoir of 1913, no British material of Old Palaeozoic echinoderms was treated monographically by Bather. But we are indebted to him for short but valuable papers on certain British edrioasteroids (Bather 1900, 1915). The work on the Silurian crinoids which he planned was never executed except for a series of minor

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contributions (Bather 1890-2; 1896; 1906; 1907). Much useful information about British forms can, however, be obtained from the only part published of his monograph of the Crinoidea of Gotland (Bather 1893). The non-crinoid Pelmatozoa have thus attracted relatively slight attention after the middle of the nineteenth century when they were described by Edward Forbes (1848) in a memoir which was very good for its time. A certain number of species of the abundant crinoid fauna in the Wenlock Limestone were illustrated by Murchison (1839) in *The Silurian System* and briefly described by Phillips. In spite of Bather's papers just referred to there is no doubt that the crinoids still offer a fertile field of research, as evidenced by the recent publications by Dr. Ramsbottom (1950, 1951, 1952, 1958).

The only Ordovician and Silurian echinoderms included in the monographs of the Palaeontographical Society are the Asterozoa. These have been treated in a comprehensive volume—unfortunately not completed—by W. K. Spencer, published between 1914 and 1940. It tells us much about the difference in character between the British and the Balto-Scandian echinoderm faunas of the Old Palaeozoic that a corresponding work could not have done on the basis of Balto-Scandian material. For fossil remains of asteroids and ophiuroids are met with only occasionally in the deposits of Scandinavia and of the East Baltic area.

On the other hand, where Balto-Scandia is concerned, cystoids have clearly been a conspicuous element in certain Middle and Upper Ordovician faunas. Crinoids have been found in great abundance particularly in the Silurian of Gotland. A first orientation as to the diversification in each group was presented by Angelin's classical work, edited posthumously in 1878. Through his monograph of the crinoids of Gotland, Bather (1893) made a skilful and badly needed revision of the inadunate forms. The articulate crinoids of Gotland (and of Britain) were accounted for by Springer, in 1920, but the camerates have had to wait much longer. Lately, however, Professor Ubaghs, of Liège, has taken up their study. The work is well under way, and three parts have been published (Ubaghs 1956-8). Other recent contributions to the knowledge of the Old Palaeozoic echinoderm fauna of Scandinavia mainly concern different non-crinoid groups. It should be mentioned that even Jaekel drew on material in the Swedish Museum of Natural History in Stockholm when preparing his great monograph of the Pelmatozoa (1899).

The Ordovician of Estonia and of the Leningrad district is famous for excellently preserved and, in part, unique echinoderms, first and foremost non-crinoid pelmatozoans. Many of these were early described in the classic works of Pander (1830), Leuchtenberg (1843), Volborth (1846, &c.), Eichwald (1860, &c.), and Friedrich Schmidt (1874, &c.). Fresh light has been thrown on the morphology and taxonomy of many remarkable forms by the eminent investigations of Professor Hecker (1923, 1940, 1958, &c.), of Moscow. Two interesting genera of Ordovician crinoids have been commented upon by Professor Öpik (1934, 1935), then in Tartu, but the crinoids of the East Baltic Palaeozoic are comparatively poorly known so far.

What has been said now is of course in no way a complete review of the available literature on Old Palaeozoic echinoderms in Britain and Balto-Scandia. My intention has only been to give a rough sketch of the literary background of our subject. It may be added that summaries of the regional distribution of some groups of pelmatozoans are included in general works, as those of Barrande (1887) and Jaekel (1899). Special men-

tion is due to the *Thesaurus siluricus* by J. J. Bigsby (1868), which is a bold attempt to indicate the main traits of Cambro-Silurian palaeobiogeography on the basis of an extensive compilation of data in the relevant literature.

#### FACTORS IN THE DISPERSAL OF ECHINODERMS

At a British Association meeting in 1938 a discussion was held on 'The Distribution and Migration of certain Animal Groups in the British Lower Palaeozoic Faunas'. The opening contribution, published subsequently in the *Geological Magazine*, was given by Dr. Stubblefield. It gave most valuable details on the behaviour of trilobites in this respect. Dr. Stubblefield (1939, p. 49) observed that 'any conclusions made at the present stage are tentative and are offered as an incentive to research'. Twenty years have passed since these words were uttered. But they are just as true now as then and will for many years to come stand as a motto for all discussions of this kind, irrespective of the group of animals dealt with.

In addition, Dr. Stubblefield drew attention to the fact that trilobites are favourable objects for the study of migration-paths, because they were presumably characterized by ecdysis. As a result, the number of potential fossils were several times greater than the number of individuals. The adult echinoderms, on the other hand, produce only one skeleton during their lifetime. It may be remembered, however, that the echinoderms have a remarkably high capacity of regeneration, which enables a rapid substitution of lost or cast-off parts of the body. Theoretically, this may have contributed to augment their share in the fossil record but in practice it may have been a rather negligible factor.

Another drawback is that the adult stages were capable of no, or a very restricted, shift of position. Like their recent representatives, the great majority of the early echinoderms were bottom-dwellers, either sedentary, as the bulk of the pelmatozoans, or moving sluggishly on the sea-floor or in the bottom ooze, or hiding in crevices of coral-reefs, and so forth. These habits may have been an advantage to potential fossils but did not favour a rapid distribution over wide areas by means of adult individuals. However, echinoderms have an extremely wide range of distribution in modern seas. The fossil record tells us that this was true also of echinoderm faunas from the Palaeozoic onwards. The explanation is, as in so many other cases where the adult generation is practically passive, that the migration to new areas of distribution and their colonization is chiefly performed by larvae. We do not know anything about the behaviour and resistibility of the larvae of primitive echinoderms. But it is reasonable to imagine that, in principle, they were much the same as those of the larvae of recent forms.

Because pelmatozoans predominated strongly among the echinoderms in the Old Palaeozoic faunas, attention should in the first case be given to their only existing representatives, the crinoids, which are likely to demonstrate conditions most nearly comparable to those of their Palaeozoic predecessors. The stage of active swimming is short in the crinoids, its duration being necessarily restricted by the fact that the larvae have no mouth and, accordingly, cannot take any nourishment. This stage lasts generally two or three days but may exceptionally be prolonged to twelve days (cf. Dawydoff 1948, p. 351). In the latter case especially the allotted time is enough for the spreading of a given species over great distances.<sup>1</sup> The larvae of certain other echinoderm groups,

<sup>1</sup> The transport of marine animals by sea currents has been discussed by Born (1920).

which were yet subordinate in Cambro-Silurian times, lead a pelagic life which may last for months.

There are very few examples of a pelagic, maybe epiplanktonic, habit in adult echinoderms; the most well known of fossil forms is the Upper Cretaceous crinoid *Uintacrinus*. In Middle Ordovician times no echinoderm reached a more universal distribution than the hydrophorid genus *Echinosphaerites*. The spherical thecae of *E. aurantium* or closely related forms are found in many parts of the world. Bather (1928, pp. lxxviii et seq.) tried to account for its relative ubiquity by the alternative explanation that the thecae were occasionally torn off from their tiny stems and swept away by waves and currents. Bather also set forth the hypothesis that thecae of dead individuals floated in the plankton to be ultimately washed ashore. It goes without saying that a nekroplankton could not contribute to the dispersal of the living *Echinosphaerites*. In view of the fact that the *Echinosphaerites*-beds give the impression of being autochthonous, Bather's theory seems to be supported by little actual evidence (see also Regnéll 1945, p. 146).

It should be mentioned, finally, that in the free-living groups of echinoderms, dispersal may to some extent be due to active migration by adult individuals. Schindewolf (1950, p. 54) quoted an instance where marked specimens of asteroids had been stated to migrate more than a thousand kilometres in a remarkably short time.

On the whole, the ways in which echinoderms spread and which have secured them a prominent position in practically all types of biotopes in recent seas all over the world, are of little help to the sleuth who seeks to follow their track through the ancient seas. But the echinoderms have a quality which is much to their credit as potential fossils, that is to say the heavy skeleton characteristic of most of their representatives. This armour, which was in many cases disintegrated after the death of the animal, was no doubt extremely resistant to destructive agencies. Thus, we have reason to suppose that the quota of echinoderm remains in the fossil record is greater, rather than the reverse, than the quota of echinoderms in the faunal assemblages once living. This leads us to the conclusion that the numerous occasions in which a species is represented in our collections by a very small number of specimens, or maybe by a unique specimen, reflect an original condition: the species will have been of very scarce occurrence in the biota to which it belonged.

#### EDRIOASTEROIDS

Edrioasteroids have never played any conspicuous role in the faunas inhabiting the Cambro-Silurian seas which covered the areas now under discussion. From the Cambrian there are only one or two isolated finds of *Stromatocystites balticus* Jaekel. This species has unfortunately not been encountered in the solid rock but in erratic boulders in north Germany. According to Jaekel (1899, p. 42), these boulders originate from the Middle Cambrian *Paradoxissimus* Sandstone of the Baltic Basin exposed on Öland. Previously the specimens were in museums in Germany, but it is to be feared that they have been lost. *Stromatocystites*, which has not been found in Britain, seems to be of North American origin, since it has been recorded in the Lower Cambrian of Newfoundland.

The evolution of the edrioasteroids reached its acme during the Middle Ordovician. This is due almost exclusively to the prolificity of the North American stock, mainly the Hemicystitidae. The very scanty material from the East Baltic area includes mainly

Lower Ordovician forms. The peculiar *Pyrgocystis* is represented by three species, the age of which is not precisely known, but the specimens seem to originate from beds corresponding to the Arenig (Hecker 1939, p. 245). It is possible that *Pyrgocystis* was present in the Ordovician of the Oslo region as well. Unfortunately, it has not been possible to locate the specimen referred to incidentally by Jaekel in 1927 (cf. Regnéll 1948, p. 39, footnote 2). Dr. G. Henningsmoen has kindly informed me that there is nothing of that kind in the collections of the Paleontologisk Museum in Oslo.

In Great Britain *Pyrgocystis* has been found in the Ashgillian Starfish Bed in Girvan, and in the Wenlock Shales of Shropshire (Bather 1915, p. 16). By which migration routes *Pyrgocystis* arrived at the British area is not entirely evident, because the genus has also been found in Blackriveran beds of Minnesota, which may be correlated broadly with the basal Caradoc. But it is justifiable to state that the Ordovician centre of dispersal of *Pyrgocystis* was located in the East Baltic area. As has just been mentioned, the genus is represented in the Wenlock of England. Other Silurian localities exist on Gotland and in the State of New York. Whether the Silurian forms are descendants of their Ordovician predecessors within the respective regions, or whether they have been introduced by a new faunal invasion, is not known.

There is other evidence of the Baltic origin of the turret-shaped edrioasteroids. This is supplied by *Cyathotheca*, which is known from the Vaginatum Limestone, on the Arenig-Llanvirn boundary, and from the top of the Ordovician in Dalecarlia, North-Central Sweden. In addition, the Middle Ordovician of Estonia has yielded two species of *Cyathocystis*. Like *Cyathotheca* this genus is absent in the British fossil record, but there are two species of *Cyathocystis* in the American Ordovician (*C. americana* Bassler 1936, *C. oklahomae* Strimple and Graffham, in Strimple 1955). This would indicate a faunal interchange in Ordovician times between the Baltic area and North America via the Polar Basin.

It is interesting that the disk-shaped type of edrioasteroids, which is the predominating type in North America and Central Europe, is almost unrepresented in the areas now under discussion. The only exception is *Edrioaster buchianus* from a Bala sandstone in Denbighshire, North Wales.<sup>1</sup> This find is remarkable also from the point of view that the four other known species of *Edrioaster* occur in the Trenton of North America. It is inadvisable to give any opinion of the direction of the migration, since *E. buchianus* and the American species seem to have been roughly contemporaneous.

In another context (Regnéll 1950, pp. 10-12) I have commented briefly on the biogeographical significance of edrioasteroids in general.

#### CARPOIDS

The stratigraphical and geographical distribution of the carpoids<sup>2</sup> neatly display—or seem to do so—the existence of four subsequent faunas, each with a characteristic

<sup>1</sup> The exact locality was given by Bather (1900, p. 194) as 'two miles west of Yspetty Evan [Yspetty Ifan, acc. to the Geol. Surv. "Quater-Inch" map, sheet 9 & 10]; that is to say, about two miles south of Pentre Voelas [Pentre Foelas], and therefore in Denbighshire and not in Caernarvonshire as stated by J. W. Salter—and by R. Etheridge, sen.—'. The present writer has not been able to find out if the 'Caradoc beds', referred to by Bather, are Caradoc in the modern sense of this term or if they belong to the Upper Bala or Ashgill.

<sup>2</sup> The carpoids are here taken in the conventional sense of the term, thus including aberrant forms as *Lingulocystis* Thoräl (cf. Chauvel 1941, p. 172).

regional localization. For the sake of convenience, these faunas will be designated by the names of predominating carpod genera, as follows: 1, The Middle Cambrian *Trochocystites* fauna; 2, the Ordovician *Dendrocystites* fauna; 3, the Silurian *Placocystites* fauna; and 4, the Lower Devonian *Anomalocystites*-*Australocystites* fauna. Faunal hiatuses occur in the Upper Cambrian, in the basal Silurian, and in the Ludlow, but these blanks are outstepped by some genera.

The oldest fauna, which comprises two or three genera beside *Trochocystites*, is likely to have originated in the Bohemian Basin but rapidly invaded the waters over south France, Spain, and Morocco. The *Dendrocystites* fauna occupied a much larger area, and the number of genera were multiplied. This fauna represents a high-watermark in carpod evolution. From the faunal province inhabited by the Middle Cambrian forms, carpoids spread to Estonia in early Ordovician times and reached North America in Chazyan times (Llanvirn-Llandeilo). This presumably took place via a Polar route, as there are no records at all from Ireland, and only from Caradocian-Ashgillian deposits in Scotland and England. All carpoids from Estonia described so far belong to *Rhipidocystis*. This genus, which seems to be endemic to the East Baltic area, comprises six or seven species, probably ranging from the Arenig to the Caradoc.

Carpoids are practically unrepresented in the Ordovician faunas of England. The only published record seems to be a species from the Middle Ashgillian *Dalmanitina robertsi* Beds in the Cautley District, Yorkshire, which, with a question-mark, was referred to *Ateleocystites*<sup>1</sup> by Marr (1913, p. 4).

The famous Starfish Bed of Ladyburn in Girvan has yielded two species of *Cotlurnocystis* and one species which was described by Bather (1913) as *Dendrocystis scotica* but which was later given the rank of an independent genus called *Dendrocystoides*. These are among the last survivors of the Middle European *Dendrocystites* fauna. *Dendrocystoides* developed from *Dendrocystites*, and the remarkable *Cotlurnocystis* has an early representative in *C. primaeva* of Languedoc which is probably of early Arenig age (Thoral 1935, p. 100). It should be mentioned that remains of carpoids are practically non-existent in the Ordovician rocks of Scandinavia. There is an isolated record of a stem-fragment in a boulder—probably Ashgillian—found on Öland. This has been assigned to *Dendrocystites* (Regnéll 1945, p. 194).

The next younger carpod assemblage, the *Placocystites* fauna, is of particular interest to us, being restricted to England on the one hand and Gotland on the other. Two species have been described from the Wenlock Limestone in Dudley, namely *Placocystites forbesianus* Koninck 1869 (syn. *Ateleocystis gegenbauri* Haeckel 1896), and *Ateleocystites fletcheri* Salter 1873. According to Woodward (1880, p. 195), the species mentioned are identical, as was also stated by Barrande (1887, p. 90). No recent authors seem to have commented upon *Ateleocystites fletcheri*, but the species has been entered under this name in the well-known *Bibliographic and Faunal Index* by Bassler and Moodey (1943, p. 132). Unfortunately, I have not seen any actual fossil material either of the so-called *Ateleocystites fletcheri*, or of the Caradocian *Ateleocystites luxleyi* Billings type of the genus, from the Trentonian of Canada. But a comparison between the North

<sup>1</sup> When studying material in the collections of the Geological Survey and Museum, London, the present writer noticed, many years ago, two specimens from Shoalhook (presumably from the Lower Ashgill Shoalhook Limestone), one of which is labelled '*Ateleocystites oblongus* Ms.' and the other '*Ateleocystites* n.sp.'. The specimens have not been examined.

American type species as figured by Miss Alice E. Wilson (1946, pl. 2, figs. 1-4), and *Ateleocystites fletcheri* as figured by Salter (1873, p. 128), makes it clear that the two forms cannot possibly be congeneric. Instead, *Ateleocystites fletcheri* has to be transferred to *Placocystites*. It may well be that it is in fact identical with *P. forbesianus*, as suggested by Woodward and Barrande. If this is true, there is only one carpod species from the English Wenlock.

If there be some doubt about the species erected by Salter, we have, so far, no substantial knowledge of the member of the *Placocystites* fauna found on Gotland. It is represented by one specimen. It is not known exactly from which stratigraphic unit it comes, but it is reasonable to assume that the specimen originates from a stratum equivalent to some part of the Wenlock Limestone. According to information received from the late Professor T. Gislén, of Lund, it should be assigned to a new species related to *Placocystites forbesianus* (cf. Regnéll 1945, pp. 196-7).

As mentioned, this uniform carpod fauna seems to have occupied a well-defined marine province in west and north-west Europe, no Silurian carpoids being known from any other part of the world. It is a ticklish question to say from where the *Placocystites* fauna was introduced. Among pre-Silurian carpoids there is not one which can be safely referred to *Placocystites*. It is true that *Anomalocystites bohemicus* Barrande from Ashgillian beds of Bohemia belongs to this genus according to Chauvel (1941, p. 215), but Caster (1952, p. 88) believes it may prove to be an Ateleocystitidae. Be that as it may, the Bohemian form is the only member of the Placocystitida in the Ordovician of Europe, while these enjoyed a certain flourishing in North America. Taking into view the considerable difference in age between the Silurian *Placocystites* and their plausible Ordovician progenitors, we must leave the question whether the *Placocystites* fauna was of an easterly or of a westerly origin unanswered. The fauna appeared rather abruptly. Its closest affinity is with Lower Devonian forms. We are thus entitled to assume that England was the prime centre of dispersal of the widespread fourth carpod fauna (the *Anomalocystites-Australocystis* fauna), of early Devonian age, which meant a remarkable revival of the carpod stock before its final extinction.

#### EOCRINIDS AND PARACRINIDS

An analysis of the stratigraphic and regional distribution of the eocrinoids leads us to conclude that the mainly Middle Cambrian *Eocystites* fauna originated in North America in early Cambrian time. No members of this fauna have been traced in the areas now under discussion, although they were present in the Bohemian Basin and France. An interesting find of a new eocrinoid of late Middle Cambrian or early Upper Cambrian age from the Lena Basin in east Siberia was recently announced by Yakovlev (1956).

The eocrinoids rapidly colonized new marine provinces, however, and the *Macrocybella-Mimocystites* fauna seems to have been distributed nearly all over the world in Tremadocian time. But it is worth noticing that Balto-Scandia, which was later to become a refuge of the declining eocrinoid stock, does not seem to have been inhabited by the fauna just mentioned. In England this fauna is represented by *Macrocybella mariae* in the Shineton Shales, the only eocrinoid recorded so far from the British Isles.

The *Macrocybella-Mimocystites* fauna had laggards right up to the close of the Ordovician but was largely substituted by a fauna containing *Cryptocrinites*, *Bockia*, *Ascocystites*, and *Polyptychella*, at the same time as the centre of eocrinoid distribution

was shifted to Balto-Scandia, and especially to the East Baltic area. There several species of *Cryptocrinites* and *Bockia* are found, ranging from the Arenig to the Lower Caradoc.

In Europe the eocrinoids became extinct before the opening of the Silurian. They definitely terminated with two species of the inadequately known *Lysocystites* in the upper Niagaran (Wenlock). This is, moreover, a strangely isolated occurrence of eocrinoids in North America, since *Lysocystites* is separated from the next-older eocrinoids by a time-gap extending to the Middle Cambrian.

The paracrinoids are an almost negligible quantity in the Lower Palaeozoic faunas outside east North America. Whereas there are a dozen American genera, ranging from the Chazyan Crown Point Formation (inclusive) (approximately on the Llanvirn–Llandeilo boundary) to the Trentonian Kirkfield Formation (Caradoc), the genus *Achradocystites* is unique in Estonia and in Europe as a whole. Thanks to a recent revision by Hecker (1958) based on fresh material, *Achradocystites* is now known in some detail. Its main affinities are with *Comarocystites* which belongs to the geologically youngest among American paracrinoids. The Estonian species—there are two of them, one in Keila (D<sub>II</sub>) beds, the other in Vasalemma (D<sub>III</sub>) beds—are probably slightly younger than *Comarocystites*. It follows from the regional and stratigraphical distribution pattern of the paracrinoids that *Achradocystites* may well be an Appalachian immigrant in the Middle to Upper Ordovician fauna of Estonia.

#### HYDROPHORIDS

Hydrophorids, or cystoids in a restricted sense, are a conspicuous element in the Lower Palaeozoic faunas of both the British Isles and Balto-Scandia. There is a difference, however, in that the Ordovician hydrophorid faunas of Balto-Scandia were abundant and prolific compared with those of the British Isles, whereas the reverse was true of the Silurian hydrophorid faunas.<sup>1</sup>

The most ancient faunal assemblage of hydrophorids in Balto-Scandia appeared in late Arenig time after having been preceded by a few very early forms. Characteristic of this fauna are *Cheirocrinurus* and *Echinoencrinites*, and, in addition, in Sweden, *Sphaerocrinurus pomum*. The sequence on the east side of the Baltic is notable for a number of morphologically and phylogenetically remarkable genera, like *Asteroblastus*, *Asterocystis*, *Mesocystis*, *Blastocystis*, *Protocrinites* (cf. Hecker and Hecker 1957), and others. A corresponding fauna is not present in the British fossil record.

The highest peak of the curve illustrating the representation of hydrophorids in the Ordovician of Balto-Scandia falls within the Llandeilo and the Lower Caradoc and is

<sup>1</sup> The basis of a comparison between the British Isles and Balto-Scandia would have been firmer, had the hydrophorids of the former region been the subject of a modern revision. My personal acquaintance with the actual material is fairly limited. About ten years ago I had an opportunity to skim over the collections kept in the Museum of the Geological Survey in London, and in the British Museum (Nat. Hist.). In addition, material from Girvan has been placed at my disposal by the kind agency of the late Mr. J. L. Begg, of Glasgow. Mr. M. V. O'Brien and Mr. G. J. Murphy have permitted me to study all the cystoids from the Irish Ordovician present in the collections of the Geological Survey of Ireland in Dublin. It is true that generally the material is not very attractive from a palaeontological point of view because of the poor state of preservation in many cases. But I hope that, in spite of this, somebody will take the trouble to make a general revision which will very likely prove to be worth while. Until such a revision is available we cannot go much beyond some rather generalized statements and assumptions.



caused by the *Echinosphaerites aurantium*-*Heliocrinites* fauna. There is a certain lagging of the Scandinavian forms in relation to the Estonian ones, which indicates a trend towards the west of the early Middle Ordovician hydrophorids. This migration wave probably carried East Baltic faunal elements into the waters covering parts of Wales and Ireland. As far as I have been able to find out, the fossil record of the Caradoc hardly substantiates a similar statement as regards England. The Tramore Limestones in Co. Waterford and more or less equivalent strata in Co. Wexford, south-east Ireland, have yielded a fairly rich harvest of hydrophorids. According to personal information from Mr. G. J. Murphy, of Dublin, the Tramore Limestones may be considered as being of *Nemagraptus gracilis* age. Main constituents of these oldest hydrophorid faunas of the British Isles are members of the genera *Echinosphaerites*, *Heliocrinites*, and *Cheirocrinus*. It may be objected that these are rather cosmopolitan in distribution, and that few species are common to the British Isles and Balto-Scandia. But the idea of a gradual migration in a westerly direction fits well into the general pattern of distribution of the Balto-Scandian Ordovician hydrophorids, which seem themselves to have come from the Far East (cf. Regnéll 1948c, p. 29). In this connexion it will be appropriate to recall that, as demonstrated by Stubblefield (1939, pp. 58-60), the Caradocian trilobite faunas of south-east Ireland and Girvan have both North American and Scandinavian affinities. In the case of the bulk of the hydrophorids, an American origin is inconceivable, but, as we shall see, such an origin is evinced by the presence of representatives of *Pleurocystites*.

There is no main difference between the faunas just referred to and the Ashgill faunas in Wales and England. The most fertile collecting-grounds have been Shoalshook in South Wales and the Bala Country in North Wales.<sup>1</sup> A list of fossils, including seven species of hydrophorids, has been published by Miss Elles (1922, p. 172).<sup>2</sup> The correct interpretation of some species is still obscure. But I take it almost for granted that '*Caryocystites davisii*' M'Coy is identical with *Heliocrinites balticus* of the East Baltic area. It is probable that this is true also of '*Caryocystites granatum*' of Forbes and several subsequent authors. Further, it is likely that *Echinosphaerites granulatus* M'Coy is closely related to *Echinosphaerites aurantium*. Both these species appear in the East Baltic area in lower horizons than in the British Isles. There is a third easterly element in the British Ashgill faunas, namely *Cheirocrinus interruptus* recorded by Bather (1913) in the Drummuck Group in Girvan. According to Jaekel (1899, p. 220), two specimens of *Cheirocrinus interruptus* available to him came from the vicinity of Leningrad, the stratigraphic horizon being unknown.

The East Baltic aspect of the faunas now under discussion cannot be disputed. But there are also threads leading to the western part of the European continent. Thecal plates similar to those of *Oocystis rugata* (Forbes) (syn. *Hemicosmites rugatus* Forbes, *Hemicosmites pyriformis* Forbes), a species recorded from Ireland, Wales, and England, have been found in Ashgillian beds in Belgium (Regnéll 1951, pp. 21-22) and Languedoc

<sup>1</sup> Both Shoalshook (Shole's Hook) and Bala were exploited for hydrophorids at the beginning of the nineteenth century by officers of the Geological Survey. The fossil-bearing strata at these localities were first classified as 'Llandeilo Flags'; this designation was used, e.g., by Forbes (1848). The Shoalshook Limestone and the Rhiwlas Limestone and Mudstones are now ranged with the Lower Ashgill.

<sup>2</sup> A couple of errors have crept into this list. It is not evident if '*Caryocystites granulatus* Forbes' refers to *Echinosphaerites granulatus* M'Coy, or to *Caryocystites* (i.e. *Heliocrinites*) *granatum* (Wahlenberg). For '*Sphaeronectes*', read *Sphaerocrinites*.

(Dreyfuss 1939, pp. 129–30). And *Echinospaerites* ('*Sphaeronites*') *arachnoideus* (Forbes) may have a certain affinity to *Echinospaerites barrandei belgicus* (cf. Regnéll 1951, p. 30).

A few words may be said about '*Caryocystites*' *litchi* Forbes 1848 (see Regnéll 1951, pp. 34–35). According to my notes on the original material in the Geological Survey and Museum in London, the specimen pointed out by Salter (1866, p. 286) as the 'true' '*Sphaeronites*' *litchi* can hardly be determined (Forbes 1848, pl. 21, fig. 2c; Mus. no. 7431). Other specimens associated with it recall the genus *Haplosphaeronis* with regard to the nature of the thecal pores. But in contradistinction to *Haplosphaeronis* they seem to be many-plated and approach in this respect *Eucystis*. '*Caryocystites*' *litchi* was tentatively assigned to *Eucystis* by Jaekel (1899, p. 406). The original of the specimen figured by Forbes (1848) in his pl. 21, fig. 2b (Geol. Surv. Mus. London no. 1430) is possibly a *Sphaeronites*. '*Caryocystites?*' *munitus* Forbes 1848 should possibly be referred to *Eucystis*. The genera *Eucystis* and *Haplosphaeronis* are found in Middle and Upper Ordovician rocks in Scandinavia. *Haplosphaeronis* has also been recorded in the Gembloux Shales in the Brabant Massif in Belgium (Regnéll 1951, p. 31).

The Caradoc and Ashgill of Girvan are, if not exactly unique, so very characteristic among contemporary deposits in the British Isles in having yielded a hydrophorid fauna which has in part a definitely North American stamp impressed upon it by members of the genus *Pleurocystites*. Bather (1913) described four species from the Upper Ashgillian Drummuck Group and reviewed all species of *Pleurocystites* known up to then. Two species had previously been recorded from the British Isles, namely *P. rugeri* Salter and *P. anglicus* Jaekel.<sup>1</sup> The precise horizon of the former is not known, but it has been collected at various Caradoc localities in Wales. *Pleurocystites anglicus* was so named by Jaekel, because he thought that it came from Scotland or, possibly, from South Wales! Bather (1913, p. 475, §§ 466, 468) demonstrated that it comes from Bardahessiagh, Co. Tyrone, Ireland, and concluded that it is a little younger than *P. rugeri* and a little older than the Girvan species from the Starfish Bed.

Subsequently, I have studied echinoderm material from the Caradoc Craighead Mudstone, of the Balclatchie Group, collected in Craighead quarry, Girvan, by Mr. R. P. Tripp. This material which has not yet been published, includes a new species of *Pleurocystites*.

All species of *Pleurocystites* older than those in the Caradoc and Ashgill of the British Isles are North American, with the exception of a somewhat doubtful species from China, *P. bassleri* Sun (1948, p. 6), of Llanvirn age. In North America *Pleurocystites* survived in older Richmond (i.e. older Ashgill) times. But we must conclude that one part of the stock migrated eastward so as to reach European waters in Caradoc times. As emphasized by Foerste (*in* Slocum and Foerste 1924, p. 358), the 'direction of migration of *Pleurocystites* into the British Isles is unknown'. Records of doubtful *Pleurocystites* in Ashgill rocks of Belgium indicate the extreme eastward extension of the American influence (Regnéll 1951).

If we take a general view of the European Middle Ordovician hydrophorid faunas two main geographical provinces can be recognized: one characterized by the predominance of Aristocystitidae; and a second one characterized by the absence of genera

<sup>1</sup> Jaekel (1918, p. 95) proposed a new genus, *Dipleurocystis*, for the reception of *P. rugeri* and *P. anglicus*. In my opinion, *Dipleurocystis* is weakly founded and should be rejected.

belonging to that family. The province first mentioned, which conforms with the 'province à Amphorides' of H. and G. Termier (1952, p. 381), occupied the sea south of the hypothetical Scottish-Hungarian barrier and extended to Bretagne, the south-west of Europe, and Morocco. The other province comprised the Balto-Scandian area. The hydrophorid faunas of both provinces undoubtedly originated from the Far East.

No Aristocystitidae have been found in the Lower Palaeozoic deposits of the British Isles. Nevertheless, a certain influx of Mid-European forms may have taken place, especially to the Girvan area, as demonstrated by its carpoid fauna. On the whole, Girvan has been the meeting-place of faunal elements of different origin: Balto-Scandian, Mid-European, and North American. The Bohemian element in the Upper Ordovician faunas of Britain and Ireland is borne out very strikingly by certain trilobites, as observed by several authors, most recently by J. A. Weir (1959, p. 382).

As is the case with several other echinoderm groups, the early Silurian marks a period of decline for the hydrophorids. The Wenlock Limestone in Dudley confronts us with a hydrophorid fauna of an entirely different and much more uniform aspect. Six genera have been recorded, namely *Apiocystites*, *Lepocrinites*, *Pseudocrinites*, *Staurocystis*, *Schizocystis*, and *Prunocystites*. Of these, the last two are Echinoencrinitidae, while the four others belong to the family Callocystitidae. Apart from two species in the Upper Silurian of Balto-Scandia, the English genera are the only representatives outside North America of that family, which arose in late Ordovician times. The European Callocystitidae may be descendants of North American forms. During the deposition of the Wenlock Limestone the Callocystitidae flourished in Dudley whence they wandered to Gotland and to the Island of Ösel (Regnéll 1948c, p. 42). It would seem as if a few of the immigrants returned to North America. For, both in the case of *Lepocrinites* and of *Pseudocrinites*, the former of which has two, the latter eight species in the Lower Helderberg (Lower Devonian), the oldest representatives are those present in the Wenlock Limestone.

*Prunocystites* and *Schizocystis* are specialized morphologically and isolated geographically. They have no doubt a north-easterly origin, however, because all other members of the Echinoencrinitidae are Balto-Scandian.

Except *Lovenicystis* (Callocystitidae) there is only one hydrophorid in the Silurian of Gotland, viz. *Gomphocystites gotlandicus*. Its affinities are exclusively North American.

#### BLASTOIDS

I shall not here discuss the taxonomic position of certain Lower Palaeozoic genera, which are considered by some authors to be blastoids while others define them in a different way. I am referring to the so-called Coronata. I agree with Jaekel in placing them among the blastoids. Coronate blastoids are very scarce in the fossil record of the areas with which we are now concerned. In fact, only three genera have been mentioned in the literature, each of them containing one or two species. From Sweden there are the Middle Ordovician *Paracystis* and the Upper Ordovician *Tormoblastus*, from Britain there is the Silurian *Stephanocrinus* (see Regnéll 1945, p. 193; 1948c, pp. 30, 32, 39). Additional material both from England and Sweden is in the hands of Dr. Ramsbottom.

The oldest coronate blastoid known is *Mespilocystites* which appeared in the Llanvirn in Bohemia. It is possible that the Swedish *Paracystis* and *Tormoblastus* were derived

from the Bohemian form. It is more difficult to give an opinion of the relations between the English and the North American species of *Stephanocrinus* which were roughly contemporaneous, that is to say mainly of Wenlockian age.

### CRINOIDS

The crinoids are by far the most comprehensive of all pelmatozoan groups. But they will be dealt with very cursorily, chiefly because of my insufficient personal experience of at least the Silurian forms.

We are still unable to point out the ancestors of the crinoids. Accordingly, we have no idea of the place of origin of the group. But we can say that a differentiation into principal branches must have taken place at an early date. For, it is a fact that the most ancient crinoids in Eurasia and North America were already specialized into camerate, inadunate, and flexible forms. Crinoid evolution in relation to major palaeogeographic changes has been summarized and illustrated by diagrams in a paper by R. C. Moore (1950).

To the inadunates belong crinoid remains in Lower Arenig rocks (Lower Tremadoc of Hicks) at St. David's and on Ramsey Island, South Wales, described by Hicks (1873, p. 51, pl. 4, figs. 17-20) under the name of *Dendrocrinus cambriensis*. The generic determination is hardly correct, but, though fairly imperfect, the fossil is of great interest in being probably the oldest genuine crinoid recorded so far.<sup>1</sup> The Ramsey Island material has not been subject to a modern revision. On the whole, little information on the Ordovician crinoids of the British Isles can be gathered from the literature. It would be fortunate indeed if this deficiency could be made up, and I think there is reason to expect that it will be so in the comparatively near future.

As a matter of course, crinoid ossicles are frequently met with in various rocks of the Ordovician sequence in the British Isles. A common Welsh Caradoc fossil is that generally referred to as *Glyptocrinus basalis* M'Coy. Marr (1883, p. 126) gives its horizon as 'Middle Bala'. The species should be assigned to *Rhaphanocrinus* whose oldest known member has been recorded in the upper Chazy of New York. Also *Merocrinus salopiae* Bather (1896), from Llandeilo rocks in Shropshire, has North American affinities, but in this case the British species is the older one. It is possible that '*Actinocrinus*' *wynnei* Baily and *Periechocrinites laevis* (Portlock, *non* Angelin) provide other examples of an interchange between the Ordovician crinoid faunas of North America and the British Isles, but their generic status must be verified.

The Ordovician seas of Balto-Scandia were inhabited by a group of inadunates called the Hybocrinida. These are remarkable in so far as they demonstrate a retrograde evolution of the brachial apparatus (Regnéll 1948*a*). The oldest representative of the Hybocrinida, *Baerocrinus parvus*, appears on the Arenig-Llanvirn boundary in Estonia, followed by *Revalocrinus* in the upper Llanvirn. *Hoplocrinus* sets out in the Llandeilo and reaches Sweden in early Caradoc time. *Cornucrinus*, finally, appears in the middle Caradoc and ranges to the Ashgill, inclusive. Outside Balto-Scandia, Hybocrinida have

<sup>1</sup> *Trichinocrinus* from the Table Head Limestone of Newfoundland was supposed by Moore and Laudon (*Amer. J. Sci.* 241, pp. 262-8) to be 'older than any other yet known' (p. 262). This is probably not correct. In the correlation chart of the Ordovician published by the Geological Society of America (Twenhofel *et al.*, 1954), the Table Head Formation is placed on the level with the Llanvirn (chart, column 3; text p. 284).

been found in North America only (*Hybocrinus*, *Hybocystites*). The oldest of these originates from late Chazyan rocks in Ottawa, and it is possible, therefore, that the North American Hybocrinida are immigrants from Balto-Scandia.

Very few crinoid cups have been collected in the Ordovician of Sweden. This explains why its crinoid fauna is largely unknown. This applies also to other parts of Balto-Scandia, though to a minor degree to Estonia. A number of genera seem to be endemic, namely *Esthonoocrinus*, *Metabolocrinus*, *Pentamerocrinus*, *Perittocrinus*, *Tetractocrinus* (all of Jaekel, 1902, 1918), and the morphologically remarkable *Ristnacrinus* Öpik (1934), while *Carabocrinus esthonus* Jaekel (Vasalemma, Middle Caradoc) is a member of an otherwise exclusively American genus. According to Jaekel (1918, p. 43), *Porocrinus*, which first appears in the Blackriveran of Illinois, is evidently a derivative of *Perittocrinus* (see also Foerste, in Slocom and Foerste 1924, p. 358).

In his monograph of the inadunate crinoids of Gotland, Bather (1893, p. 7) remarked that out of forty species treated by him only six are common to Gotland and England. But it should be pointed out that of ten genera recognized on Gotland, six have also been found in England. In addition, all Gotland genera but two are represented in North America, and four species are even common to these two areas. One species, *Myelodactylus* ('*Herpetocrinus*') *ammonis* (Bather), has been recorded from both Gotland (the Slite Group: Upper Middle Wenlock), Dudley (the Wenlock Shales), Tennessee, and Indiana (Laurel, Waldrom, Beach River: Lower and Middle Wenlock). In a subsequent paper, Bather (1906) discussed species of *Botryocrinus* from Gotland, Dudley, North America, and Australia;<sup>1</sup> and in another paper (Bather 1907), he commented on a *Scyphocrinites* from west Cornwall which has Bohemian affinities.

I am not going to give further details but will restrict myself to stating that a number of recent papers tend to show that the Silurian crinoid faunas of Europe had a largely North American origin, and that many genera and several species had a very wide regional distribution (Bouška 1942, 1943, 1946, 1956a, 1956b; Lowenstam 1948; Ramsbottom 1950, 1951, 1952, 1958; Ubaghs 1958; see also Regnéll 1948c, pp. 43–44). As a matter of course more or less provincial crinoid faunas had developed, but it is apparent that conditions were favourable for an interchange of faunal elements between North America, Britain, Sweden, and Bohemia.

The apogee of Silurian crinoid development in England is marked by the prolific fauna in the Wenlock Limestone. As pointed out quite recently by Dr. Ramsbottom (1958, p. 106), this gave place to a much impoverished fauna in Ludlow times.

#### ELEUTHEROZOA

Eleutherozoa are very subordinate in the Lower Palaeozoic rocks of Balto-Scandia, while asterozoans are remarkably abundant in the Ordovician and Silurian sequences in the British Isles. 'Starfish Beds' occur in the Ashgillian Drummuck Group in Girvan; in Wenlock beds of Gutterford Burn, Pentland Hills; in Lower Ludlow shales at Church Hill, Leintwardine in the Welsh Borderland, and near Kendal, Westmorland; and in the Upper Ludlovian Kirkby Moor Flags in the Lake District, &c. Thanks to the monograph by W. K. Spencer (1914–40) we have an excellent knowledge of the Ordovician

<sup>1</sup> The Melbourne Series, in which *Botryocrinus longibrachiatus* has been found, is placed by T. W. E. David (*The Geology of the Commonwealth of Australia*, London 1950, I, tab. xi facing p. 224; see also p. 186) in the Wenlock and Lower Ludlow.

and Silurian asterozoans of the British Isles. On two occasions Spencer (1938, 1950) discussed the palaeobiogeographical aspects offered by these forms. The main facts found to be relevant for the British asterozoan fauna can be summarized as follows: the scanty Arenig and Llanvirn fauna from Wales and the Welsh Borderland 'shows a distinct affinity with that of Bohemia' (Spencer 1950, p. 396). The Middle Ordovician asterozoans covered a very wide area extending from Turkestan to the St. Lawrence valley. This was literally true of the Welsh and Irish *Stenaster*, and of *Protopalaeaster*, from the Welsh Borderland. Other genera occurring in the British Isles have also been met with either in the west or the east of this vast marine province. 'The centre of much of the new differentiation appears to be to the west of Britain' (Spencer 1950, p. 398). The basic difference between Welsh Ashgillian faunas and contemporary faunas of Girvan is apparent also from the fact that the latter have abundant starfish while the former have none. Spencer (1950, pp. 401-2) recognized four elements in the Girvan starfish fauna, namely forms derived from Middle Ordovician ancestors in the same basin; new forms derived from one or two centres, which supplied immigrants to North America as well; new forms derived from the Arenig faunas of South France; and 'immigrants with untraced ancestry, found also in the Silurian of Australia'. The affinity to Australian faunas persisted during the Silurian.

Turning to Balto-Scandia we find that no information whatsoever about Ordovician asterozoans can be derived from the literature. I can add but little to this, but would like to mention that available to me is a poor specimen of an asterozoan (undescribed) from Upper Ordovician *Tretaspis* beds in Vestrogothia (Västergötland), Sweden. In an erratic boulder of a rock from the Caradoc *Coelosphaeridium* zone in the Oslo area, Norway, Dr. G. Henningsmoen has detected remains of starfish (undescribed).

Three species have been recorded from the Silurian of Gotland. These are *Neopalaeaster hesslandi* H. W. Rasmussen (1952) from Upper Llandovery beds near Visby; *Urasterella ruthveni leintwardinensis* Spencer (1918, p. 147) from Wenlock beds; and *Palasterina antiqua* (Hisinger) (see Spencer 1922, p. 229) from Upper Ludlow beds of south Gotland. Notable among material which still remains to be described is a magnificent specimen of an ophiuroid from the so-called *Pterygotus* Beds at the top of the Höglint Group (Lower Wenlock), Visby.

Rasmussen (1952, p. 23) is inclined to derive *Neopalaeaster* from the Ordovician *Siluraster*, represented in Bohemia and North Wales (*S. caractaci* (Gregory)). *Urasterella* is first found in the Middle Ordovician of North America (Spencer 1918, p. 136). It is also present in the Ashgill of Girvan, in the Wenlock of the Pentland Hills, and in the Upper Ludlow of the Lake District. *Palasterina*, finally, has been found in the Middle Silurian of Australia and England, and in the Upper Ludlow of the Lake District (Spencer 1950, p. 402; see also Regnéll 1948c, p. 44).

The remaining eleutherozoic groups do not require any time-consuming comments.

No remains of undoubted holothurians have been recognized in the Lower Palaeozoic rocks of our areas.<sup>1</sup> We may expect, however, that sclerites of holothurians will be found in the residue of samples treated with acetic acid, or in wash samples.

<sup>1</sup> *Eothuria beggi* MacBride and Spencer 1938, from the Ashgill of Girvan, described as a holothurian has by most subsequent authors been considered to be an echinoid. Gutschick (1954) evidently accepted the original interpretation as a holothurian. Durham and Melville (1957, pp. 262-3) classify the Megalopoda (order containing *Eothuria* only) as 'Incertae sedis'.

Both Britain and Balto-Scandia have yielded forms which have a bearing on the early phylogeny of the echinoids. From the Ashgill of Girvan come the remarkable *Aulechinus* and *Ectinechinus*, while Durham and Melville (1957, pp. 243–4) have recently presented evidence of a Silurian age of *Myriastiches*, possibly from the Welsh Borderland. In any case, the Scottish genera mentioned are the most ancient of the Lepidocentroida. It would seem that this order had a centre in Britain. Silurian representatives are ‘*Wrightia phillipsiae*, *Lepidocentrus?* sp., *Echinocystites pomun*, and *Palaeodiscus ferox* (listed by MacBride and Spencer 1938, p. 93; cf. Regnéll 1956, p. 156). The only Silurian species from outside the British Isles is *Kouinekocidaris silurica* from the State of New York. This species was approximately contemporaneous with ‘*Wrightia*’ (Upper Llandovery) which is the oldest of the British species.

In their paper just referred to, Durham and Melville (1957, pp. 242–4) argue that the much-disputed *Bothriocidaris*, from the upper Middle Ordovician and Upper Ordovician of Estonia, is a genuine echinoid. A common ancestor of the geographically isolated *Bothriocidaris* and the lepidocentroids is not known. Irrespective of which interpretation we adopt for *Bothriocidaris* we cannot doubt that this very singular unit ended in a blind alley.

A more prosperous line of development, namely that of the Melonechinoida, can be traced back to the Silurian (probably the Lower Ludlow) of Gotland. *Gotlandechinus* described recently (Regnéll 1956) is the most ancient member of this order. In addition, spines of cidaroids and other echinoid remains not safely assigned to definite higher categories, have been found in the Silurian rocks of Gotland. We have no idea of the common source—if there was any—of the lepidocentroids and the melonechinoids, nor, in consequence, of their breeding ground.

Much of the early history of the echinoids seems to have been enacted in the Old Palaeozoic seas of Balto-Scandia and Britain. This is true also of the *ophiocistioids*, very rare eleutherozoic forms which unite traits of several echinoderm groups. It is possible that they evolved in the East Baltic area, for the genus *Volchovia* appeared there as early as in Arenig times. Two species have been described from the Leningrad province (Hecker 1938, 1940), and a slightly younger one from the Oslo district, Norway (Regnéll 1948b). There is a great discontinuity in the development of the Ophiocistioidea as known to us, as the next younger representative of the class, *Euthemon*, is not met with until in the Wenlock Limestone of the Malvern district (Sollas 1899, p. 696). Two more genera, each with one species, have come from British Silurian rocks, namely *Eucladia* from Sedgley, near Dudley (Woodward 1869, p. 241), and *Sollasina* (genotype: *Eucladia woodwardi* Sollas 1899) from Leintwardine (Sollas 1899, p. 695). Both are probably Lower Ludlovian of age. A last survivor of the Ophiocistioidea (*Rhenosquama* R. Richter 1930) has been traced in the Middle Devonian of the Rhine Valley, Germany. The group became extinct without leaving any descendants.

#### INCERTAE SEDIS

Finally, a few words shall be said of *Cyclocystoides* and *Bolboporites*, echinoderms of problematic nature.

As regards *Cyclocystoides* it may suffice to refer to a diagram published by me (Regnéll 1948c, p. 41), showing the regional distribution and approximate stratigraphic

range of the known species of *Cyclocystoides*.<sup>1</sup> It is apparent that *Cyclocystoides* originated in North America in early Middle Ordovician time. Migrants moving in an easterly direction turned up in Caradoc faunas in England, and in Ashgill faunas in Girvan. The genus entered Gotland in the Wenlock.

*Bolboporites* has a very narrow stratigraphic range in Balto-Scandia, occurring in Arenig-Caradoc beds. It has been recorded both from the East Baltic area, Sweden, and Norway. A faunal interchange with North America is evidenced by the fact that *Bolboporites* has been found in the Chazy and Blackriveran of Canada and the State of New York. The only additional record of *Bolboporites* relates to the Tramore Limestones (Caradoc) of south-east Ireland (Reed 1899, p. 732).

#### EPILOGUE

The various facts presented here will serve to illustrate the points of contact, and the differences, between the echinoderm faunas of the Lower Palaeozoic rocks in the British Isles on the one hand and in Balto-Scandia on the other. To be sure, it is no easy task to recognize the individual threads in this entangled web. An oversimplification would perhaps make us believe that much of the faunal migrations were directed towards the west in Ordovician times and towards the east in Silurian times. But the pictures of palaeobiogeographical features in remote times which we endeavour to envisage are poor in details, on account of scanty information—not least of the role played by ecological factors—and vague in outline, on account of our inability to reproduce the subject in a correct perspective. Some few future finds may have far-reaching consequences. But isn't it so that what makes Palaeontology such a fascinating study is, in part, the very fact that so much of the Past remains to be revealed in the Future?

#### REFERENCES

- ANGELIN, N. P. 1878. *Iconographia Crinoideorum in stratis Sueciae siluricis fossilium* (ed. G. Lindström and S. Lovén). Holmiae.
- BARRANDE, J. 1887. Classe des Échinodermes. Ordre des Cystidées, publ. par W. Waagen. *Syst. sil. du Centre de la Bohême*, (1) 7, 1, 1–233, pl. 1–39. Prague.
- BASSLER, R. S. and MOODEY, M. W. 1943. Bibliographic and faunal index of Paleozoic pelmatozoan echinoderms. *Geol. Soc. Amer. Spec. Pap.* 45, 1–734.
- BATHER, F. A. 1890–2. British fossil crinoids, 1–8 [Inadunata, chiefly Silurian]. *Ann. Mag. Nat. Hist.* (6), 5, 306–10, 310–34, 373–88, 485, 486, pl. 14–15; 6, 222–35, pl. 10; 7, 35–40, pl. 1, 389–413, pl. 12; 9, 189–94, 194–202, 202–26, pl. 11–13.
- 1893. The Crinoidea of Gotland. 1. The Crinoidea Inadunata. *K. Sv. Vet.-Akad. Handl.* 25, 2, 1–200, pl. 1–10.
- 1896. *Merocrinus Salopiae*, n.sp., and another crinoid, from the Middle Ordovician of West Shropshire. *Geol. Mag.* (4) 3, 71–75.
- 1900. *Edrioaster buchianus* Forbes sp. *Ibid.* 7, 193–204, pl. 8–10.
- 1906. The species of *Botryocrinus*. *The Ottawa Naturalist*, 20, 93–104.
- 1907. The discovery in West Cornwall of a Silurian crinoid characteristic of Bohemia. *Trans. Roy. Geol. Soc. Cornwall*, 13, 191–7.
- 1913. Caradocian Cystidea from Girvan. *Trans. Roy. Soc. Edinb.* 49, 2, 6, 359–529, pl. 1–6.
- 1915. *Pyrgocystis* n.g. *Geol. Mag.* (6) 2, 5–12, pl. 2–3.

<sup>1</sup> Additional Devonian material published subsequently by Dr. Hertha Sieverts-Doreck (1951) does not affect the distributional pattern outline in the diagram.



- BATHER, F. A. 1928. The fossil and its environment. An Address to the Geological Society of London at its Anniversary Meeting on the seventeenth of February, 1928. *Quart. J. Geol. Soc. London*, **84**, lxi–xcviii.
- BIGSBY, J. J. 1868. *Thesaurus Siluricus. The flora and fauna of the Silurian period*. London.
- BORN, A. 1920. Die Bedeutung der Meeresströmungen für die geologische Zeitrechnung. *Ber. Senckenb. Naturf. Ges.*, **50**, 207–17.
- BOUŠKA, J. 1942. Krinoidengattung *Pycnosaccus* Angelin im böhmischen Silur. *Mitt. Tschech. Akad. Wiss.* **52**, 21, 1–3, pl. 1.
- 1943. Die Vertreter der Gattung *Gissocrinus* Angelin im böhmischen Silur. *Ibid.* **53**, 44, 1–9, pl. 1.
- 1946. On Crotalocrinitidae (Angelin) from the Silurian and Devonian of Bohemia. *Bull. Int. Akcad. Tchèque Sci.* **47**, 4, 1–17, pl. 1–4.
- 1956a. O rodu *Protaxocrinus* Springer (Crinoidea) ze středočeského siluru. *Sborník Ůstř. Ůst. Geol.* **22** (1955) (Odd. paleont.), 323–33, pl. 25 [Engl. summary at pp. 10–11; On the occurrence of the genus *Protaxocrinus* (Crinoidea) in the Silurian of Bohemia.]
- 1956b. Pisocrinidae Angelin českého siluru a devonu (Crinoidea). *Roz. Ůstř. Ůst. Geol.* **20**, 1–138, pl. 1–6. [Engl. summary at pp. 97–138; Pisocrinidae Angelin from the Silurian and Devonian of Bohemia (Crinoidea).]
- CASTER, K. E. 1952. Concerning *Enoploura* of the Upper Ordovician and its relation to other carpoïd Echinodermata. *Bull. Amer. Paleont.* **34**, 71–126, pl. 5–8.
- CHAUVEL, J. 1941. Recherches sur les cystoïdes et les carpoïdes armoricains. *Mém. Soc. Géol. Min. Bretagne*, **5**, 1–286, pl. 1–7.
- DAWYDOFF, C. 1948. Embryologie des échinodermes, in *Traité de Zoologie* (ed. by P.-P. Grassé), **11**, Paris.
- DREYFUSS, M. 1939. Les cystoïdes de l'Ordovicien supérieur du Languedoc. *Bull. Soc. Géol. France*, (5), **9**, 117–34, pl. 10–12.
- DURHAM, J. W. and MELVILLE, R. V. 1957. A classification of echinoids. *J. Paleont.* **31**, 242–72.
- EICHWALD, E. 1860. *Lethaea Rossica ou Paléontologie de la Russie*. **1**, Stuttgart.
- ELLES, G. L. 1922. The Bala Country: its structure and rock-succession. *Quart. J. Geol. Soc. London*, **78**, 132–75, pl. 2.
- FORBES, E. 1848. On the Cystidae of the Silurian rocks of the British Islands. *Mem. Geol. Surv. Great Brit. and Mus. Pract. Geol.* **2**, 483–534, pl. 11–23.
- GUTSCHICK, R. C. 1954. Holothurian sclerites from the Middle Ordovician of northern Illinois. *J. Paleont.* **28**, 827–9.
- HECKER, E. L. and HECKER, R. F. 1957. O novom vide roda *Protocrinites* Eichwald [On a new species of the genus *Protocrinites* Eichwald]. *Ezhegodnik Vsesoyuzn. Paleont. Obsch.* [Ann. Soc. Paléont. URSS], **16**, 274–8, 1 pl. [Russian].
- HECKER, R. F. 1923. Ekhinosferidi ruskogo silura [Echinospaeritidae of the Silurian of Russia]. *Trudi Geol. Mineral. Muz. Petra Velikogo Ross. Akad. Nauk (Trav. Mus. Géol. Minéral. Pierre le Grand Acad. Sci. Russ.)* **4** (1919–23), 1–63, pl. 1–2 [Russian].
- 1938. A new member of the class Ophiocistia Sollas (*Volchovia* n.g.) from the Ordovician of Leningrad Province and changes in the diagnosis of this class. *C.R. (Doklady) Acad. Sci. URSS*, **19**, 425–7.
- 1939. *Pyrgocystis* iz nizhnego silura Leningradskoy oblasti. *Izv. Akad. Nauk SSSR (Bull. Acad. Sci. URSS)*. 1939. *Otdel. biol. nauk (Classe Sci. Biol.)*, 241–6, pl. 1 [Engl. summary at pp. 245–6; *Pyrgocystis* from the Ordovician of Leningrad Province.]
- 1940. Carpoidea, Eocrinoidea i Ophiocistia nizhnego silura Leningradskoy oblasti i Estonii, in Hecker, Nizhnesiluriyskie i devonskie iglokozhié (Ordovician and Devonian echinoderms). *Akad. Nauk SSSR. Trudi Paleont. Inst.* **9**, 4, 5–82, pl. 1–10. [German summary at pp. 56–76; Carpoidea, Eocrinoidea und Ophiocistia des Ordoviziums des Leningrader Gebietes und Estlands.]
- 1958. Novie dannie o rode *Achradocystites* (Echinodermata, Paracrinoidea). *ENSV Tead. Akad. Geol. Inst. Uurimused*, **3**, 145–63, pl. 1–3. [German summary at pp. 161–2; Neues über die Gattung *Achradocystites* (Echinodermata, Paracrinoidea).]
- HENBEST, L. G. 1952. Significance of evolutionary explosions for diastrophic division of Earth history —introduction to the symposium. *J. Paleont.* **26**, 299–318.

- HICKS, H. 1873. On the Tremadoc rocks in the neighbourhood of St. David's, South Wales, and their fossil contents. *Quart. J. Geol. Soc. London*, **29**, 39–52, pl. 3–5.
- JAEKEL, O. 1899. *Stammesgeschichte der Pelmatozoen*. **1**, *Thecoidea und Cystoidea*. Berlin.
- 1918. Phylogenie und System der Pelmatozoen. *Paläont. Z.* **3**, 1–128.
- KALJO, D. *et al.* 1956. Eesti NSV ordoviitsiumi fauna nimestik. II. Keskordoviitsium. [A list of the Ordovician fauna of the Estonian USSR. II. Middle Ordovician.] Echinodermata (by A. RÕDMUSOKS) at pp. 13–15. *Loodus. Selts Eesti NSV Tead. Akad. Juur. Abiks Loodus*, **25**, 1–63. Tartu. [Estonian and Russian.]
- LEUCHTENBERG, M. HERZOG VON, 1843. *Beschreibung einiger neuen Thierreste der Urwelt aus den silurischen Kalkschichten von Zarskoje-Selo*. St. Petersburg.
- LOWENSTAM, H. A. 1948. Biostratigraphic studies of the Niagaran inter-reef formations in northeastern Illinois. *Illinois State Mus. Sci. Pap.* **4**, 1–146, pl. 1–7.
- MACBRIDE, E. W. and SPENCER, W. K. 1938. Two new Echinoidea, *Aulechinus* and *Ectinechinus*, and an adult plated holothurian, *Eothuria*, from the Upper Ordovician of Girvan, Scotland. *Philos. Trans. Roy. Soc. London (B)*, **229**, 91–136, pl. 10–17.
- MARR, J. E. 1883. *The classification of the Cambrian and Silurian rocks*. Cambridge and London.
- 1913. The Lower Palaeozoic rocks of the Cautley District (Yorkshire). *Quart. J. Geol. Soc. London*, **69**, 1–18.
- MOORE, R. C. 1950. Evolution of the Crinoidea in relation to major paleogeographic changes in Earth history. *Int. Geol. Congr. Rep. 18th Sess. Gr. Brit. 1948*, (12), 27–53.
- MURCHISON, R. I. 1839. *The Silurian System*. London.
- ÕPIK, A. 1934. *Ristnacrinus*, a new Ordovician crinoid from Estonia. With a note by F. A. Bather. *Act. Comm. Univ. Tart. (Dorpatensis)*, **28**, 8, 1–8, pl. 1–2. [Also *Publ. Geol. Inst. Univ. Tartu*. 40.]
- 1935. *Hoplocrinus*—eine stiellose Seelilie aus dem Ordovizium Estlands. *Ibid.* **29**, 1, 1–17, pl. 1–2. [Also *Publ. Geol. Inst. Univ. Tartu*. 43.]
- PANDER, C. H. 1830. *Beiträge zur Geognosie des russischen Reiches*. St. Petersburg.
- RAMSBOTTOM, W. H. C. 1950. A new species of *Lyriocrinus* from the Wenlock Limestone. *Ann. Mag. Nat. Hist.* (12), **3**, 651–6, pl. 9.
- 1951. Two species of *Gissocrinus* from the Wenlock Limestone. *Ibid.*, **4**, 490–7, pl. 9.
- 1952. Calceocrinidae from the Wenlock Limestone of Dudley. *Bull. Geol. Surv. Great Brit.*, **4**, 33–48, pl. 4–5.
- 1958. British Upper Silurian crinoids from the Ludlovian. *Palaeontology*, **1**, 106–15, pl. 20–21.
- RASMUSSEN, H. W. 1952. A new Silurian asteroid from Gotland, Sweden. *Geol. Fören. Förhandl. Stockholm*, **74**, 17–24.
- REED, F. R. C. 1899. The Lower Palaeozoic bedded rocks of County Waterford. *Quart. J. Geol. Soc. London*, **55**, 718–72, pl. 49.
- REGNÉLL, G. 1945. *Non-crinoid Pelmatozoa from the Paleozoic of Sweden*. Lund. [Also *Medd. Lunds Geol.-Min. Inst.* 108.]
- 1948a. Swedish Hybocrinida (Crinoidea Inadunata Disparata; Ordovician-Lower Silurian). *K. Sv. Vet.-akad. Arkiv f. Zool.* **40A**, 9, 1–27, pl. 1–4.
- 1948b. Echinoderms (Hydrophoridae, Ophiocistia) from the Ordovician (Upper Skiddavian, 3c $\beta$ ) of the Oslo region. *Norsk Geol. Tidsskr.* **27**, 14–58, pl. 1–2.
- 1948c. An outline of the succession and migration of non-crinoid pelmatozoan faunas in the Lower Paleozoic of Scandinavia. *K. Sv. Vet.-akad. Arkiv f. Kemi Mineral. o. Geol.* **26A**, 13, 1–55, 1 tab. in two leaves.
- 1950. 'Agelacrinites' ephraemovianus (Bogolubov) and 'Lepidodiscus' fistulosus Anderson (Edrioast.). *K. Fysiogr. Sällsk. Lund Förhandl.* **20**, 218–31 [1–14 of sep. print].
- 1951. Revision of the Caradocian-Ashgillian cystoid fauna of Belgium. With notes on isolated pelmatozoan stem fragments. *Inst. Roy. Sci. Nat. Belg. Mém.* **120**, 1–47, pl. 1–6.
- 1956. Silurian echinoids from Gotland. *K. Sv. Vet.-akad. Arkiv f. Mineral. o. Geol.*, **2**, 155–78, pl. 1–4.
- SALTER, J. W. 1866. On the fossils of North Wales [in Ramsay, A.C., The geology of North Wales]. *Mem. Geol. Surv. Great Brit. and Mus. Pract. Geol.* **3**, 239–381, pl. 1–26.
- 1873. *A catalogue of the collections of Cambrian and Silurian fossils contained in the Geological Museum of the University of Cambridge*. Cambridge.

- SCHINDEWOLF, O. H. 1950. *Grundlage und Methoden der paläontologischen Chronologie*. 3. Aufl. Berlin-Nikolassee.
- SCHMIDT, F. 1874. Über einige neue und wenig bekannte baltisch-silurische Petrefacten (Miscellanea Silurica, 2). *Mém. Acad. Sci. St.-Petersb.* (7), 21 (11), 1-48, pl. 1-4.
- SIEVERTS-DORECK, H. 1951. Über *Cyclocystoides* Salter & Billings und eine neue Art aus dem belgischen und rheinischen Devon. *Senckenbergiana*, 32, 9-30, pl. 1-2.
- SLOCOM, A. W. and FOERSTE, A. F. 1924. New echinoderms from the Maquoketa Beds of Fayette County, Iowa. *Iowa Geol. Surv. 29. Ann. Rep. 1919 and 1920*, 315-84, pl. 30-34.
- SOLLAS, W. J. 1899. Fossils in the University Museum, Oxford. I. On Silurian Echinoidea and Ophiuroidea. *Quart. J. Geol. Soc. London*, 55, 692-715.
- SPENCER, W. K. 1914-40. A monograph of the British Palaeozoic Asterozoa. *Palaeontogr. Soc.*  
 — 1938. The starfishes and cystids. *Brit. Ass. Advanc. Sci. Rep. 1938*, 415.  
 — 1950. Asterozoa and the study of Palaeozoic faunas. *Geol. Mag.*, 87, 393-408.
- SPRINGER, F. 1920. The Crinoidea Flexibilia. *Smithson. Inst. Publ.* 2501, 1-486, pl. 1-76.
- STRIMPLE, H. L. 1955. New Ordovician echinoderms. *J. Wash. Acad. Sci.* 45, 11, 347-55.
- STUBBLEFIELD, C. J. 1939. Some aspects of the distribution and migration of trilobites in the British Lower Palaeozoic faunas. *Geol. Mag.* 76, 49-72.
- SUN, Y. C. 1948. The early occurrence of some Ordovician and Silurian cystoids from western Yunnan and its significance. *Palaeont. Soc. Chiua. Palaeont. Novitates*, 1, 1-9, pl. 1.
- TERMIER, H. and TERMIER, G. 1952. *Histoire de la biosphère. La vie et les sédiments dans les géographies successives*. Paris.
- THORAL, M. 1935. *Contribution à l'étude paléontologique de l'Ordovicien inférieur de la Montagne Noire et révision sommaire de la faune Cambrienne de la Montagne Noire*. Montpellier.
- TWENHOFEL, W. H. et al. 1954. Correlation of the Ordovician formations of North America. *Bull. Geol. Soc. Amer.* 65, 247-98, 1 chart.
- UBAGHS, G. 1956a. Recherches sur les Crinoïdes Camerata du Silurien de Gotland (Suède). 1. *K. Sv. Vet.-akad. Arkiv f. Zool.* (2), 9, 515-50, pl. 1-7.  
 — 1956b. Recherches, &c. 2. *Ibid.* 551-72, pl. 1-4.  
 — 1958. Recherches, &c. 3. *Ibid.* 11, 259-306, pl. 1-5.
- VOLBORTH, A. 1846. Über die russischen Sphaeroniten, eingeleitet durch einige Betrachtungen über die Arme der Cystideen. *Verhandl. Russ.-Kaiserl. Mineral. Gesellsch. St. Petersb.*, 1845-6, 161-98, pl. 9-10.
- WACHSMUTH, C. and SPRINGER, F. 1897. The North American Crinoidea Camerata. *Mem. Mus. Coup. Zool. Harvard Coll.* 20-21, 1-837, pl. 1-83.
- WEIR, J. A. 1959. Ashgillian trilobites from Co. Clare, Ireland. *Palaeontology*, 1, 369-83, pl. 62-63.
- WILSON, A. E. 1946. Echinodermata of the Ottawa Formation of the Ottawa-St. Lawrence Lowland. *Canada Dept. Mines and Resources. Geol. Surv. Bull.* 4, 1-61, pl. 1-6.
- WOODWARD, H. 1869. On *Eucladia*, a new genus of Ophiuridae, from the Upper Silurian, Dudley. *Geol. Mag.* 6, 241-5, pl. 8.  
 — 1880. Notes on the Anomalocystidae, a remarkable family of Cystoidea, found in the Silurian rocks of North America and Britain. *Ibid.* (2) 7, 193-201, pl. 6.
- YAKOVLEV, N. N. 1956. Pervaja nachodka morskoy lilii v kembrii SSSR [First find of crinoids in the Cambrian of SSSR.] *Doklady Akad. Nauk SSSR*, 108, 726-7, 1 pl. [Russian].

PROFESSOR G. REGNÉLL  
 Paleontologiska Institutionen,  
 Lund, Sweden.